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THE CAVERNICOLOUS FAUNA OF HAWAIIAN LAVA TUBES, PART VII. EMESINAE OR THREAD-LEGGED BUGS (HETEROPTERA: REDVUIIDAE)

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ABSTRACT

This paper describes the world's second troglobitic heteropteran, Nesidiolestes sp., and presents notes on its biology. The species is restricted to the dark zones of high altitude lava tubes on Hawaii Island. Body pigmentation is lacking and the eyes are strongly reduced. This discovery again demonstrates that adaptive radiation of the epigean fauna into cave situations has occurred in Hawaii. Rather than exhibiting relictual characteristics, the species seems recently derived from a surface-dwelling (epigean) ancestor and most closely resembles the extant N. selium Kirkaldy of the same island. Epigean species of Nesidiolestes Kirkaldy have a predisposition for the cave habitat in that they are cryptic, dark-seeking, apparently nocturnal, slow-moving insects frequenting the mossy undersides of fallen logs and ferns in the rain forest. The existence of N. sp. was actually predicted on the basis of the apparently preadaptive habits mentioned. This brings the number of described troglobitic arthropods in Hawaiian lava tubes to eight species.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Many cave-dwelling emesines are known from the tropics, including species belonging to the following genera: Amilcaria, Myiophanes, Bagauda, Berlandia, Ploiaria, Lhostella, and Gardenoides. At most, they may show some eye reduction (Vandel 1965), but no significant loss of body pigmentation has occurred. Wygodzinsky (1966) in his great monograph of the world Emesinae considered all cave-dwelling species to be troglophilic. He also stressed that "in cavernicolous emesines no reduction of the eyes or loss of pigment is observed, though some species . . . are rather pale." When the biologies of these cavernicolous species are elucidated, we expect that some others will be found to be troglobitic.

Gagné and Howarth (1974) noted that they had found no prior record of a truly troglobitic species of Heteroptera, when they described the world's first such species, a mesoveliid, Speovelia sp., from a lava tube on the island of Hawaii. Thus this emesine would appear to represent the world's second known troglobitic heteropteran. Like S. sp., it appears to be restricted to a comparatively small number of lava tubes. This is in contrast to some other cavernicolous elements of the Hawaiian fauna, such as Oliarus polyphemus Fennah (Homoptera), Thaumatogryllus sp. and Caconemobius sp. (Orthoptera), Dimerogonus sp. (Diplopoda), Lycosa howarthi Gertsch (Araneae) and others. This suggests that these Heteroptera have low dispersability or are unable to colonize a greater number of lava tubes over a wider geographical area for reasons yet unexplained.

We postulated the existence of this species on the basis of the behavior of the Hawaiian epigean species and the widespread occurrence of emesines in caves throughout the tropics. Behavioral attributes of epigean Nesidiolestes species that suggest preadaptation for a cavernicolous existence are a propensity for poorly illuminated haunts, apparent nocturnal activity, slow deliberate movement, passive rather than active hunting, elongate legs and body form.

We believe that the elongate middle and hind legs in Emesinae, including N. sp., are advantageous for capturing prey. Wygodzinsky (1966) states that the wide expanse of the mid and hind legs preadapts the emesines to living on spider webs, and Readio (1927, quoting Howes, 1919) observed that in Emesaya brevipennis (Say) the elongate legs allow capture of robust and stinging prey by holding such dangerous prey clear of the substrate and its own body parts. The elongate legs allow 1) greater selection of perches, including those with widely spaced foot-holds such as tree roots and spider webs, 2) a longer and wider reach from its perch, and 3) considerable resiliency in holding onto prey until the toxic saliva takes effect.

NESIDIOLESTES KIRKALDY

Nesidiolestes Kirkaldy, 1902, Fauna Haw. 3:152.--Zimmerman, 1948, Ins. Haw. 3:129. --Wygodzinsky, 1966, Bull. Amer. Mus. Nat. Hist. 133:398.

Taxonomic description of the genus

The concept of this genus needs some alteration and expansion to contain the troglobitic species described below. The generic description presented by Wygodzinsky (1966) is our model, with the following alterations:

Body length 7-11 mm. Body with sparse to dense short setae, dorsum subglabrous. General color (in alcohol) stramineus with black markings or pallid; antennae and legs conspicuously annulate or pallid. Interocular furrow faintly to plainly bisinuate. Mesonotum and metanotum together longer than or subequal to the length of pronotum. Mesonotum length subequal to or longer than wide; metanotum length subequal to or less than width.

Fore legs as long as or longer than whole body. Posteroventral series of 1 to 5 regularly spaced large spines. Tarsus 1/9 to 1/6 the length of the tibia.

Male. Endosoma, when completely everted, with conspicuous lobes at the bases of vesica arms (FIG. 12).

TYPE SPECIES: Nesidiolestes selium Kirkaldy (monobasic).

In his generic diagnosis Wygodzinsky (1966) said of the ♀: "Seventh sternite strongly salient at middle." If this is taken to indicate that this sternite was keeled, such was not seen in N. sp., nor in the ♀♀ of N. insularis Kirkaldy and a species from Molokai.

To judge even from the very meager additional material of this genus which has been collected in the last decade from Maui and Molokai, there is further reason to believe that these apterous insects are specifically distinct on each island as Wygodzinsky (op. cit.) contended.

Key to the Species of Nesidiolestes

1. Fore femora with 6 or fewer prominent ventral spines 2
1'. Fore femora with 7 or more prominent ventral spines, epigean (Oahu I.) . . . . . insularis
2. Body and appendages pallid, no annulations; fore femora with 1 pair of prominent ventral spines; troglobitic (Hawaii I.) . . . . . N. sp.
2'. Body and appendages maculate, legs with annulations; fore femora with more than 1 pair of prominent ventral spines, epigean 3
3. Protibiae with 3 annulations, knee pale; inner, ventral aspect of profemora with 3 wide maculations (Hawaii I.)(FIG. 6) . . . . . selium
3'. Protibiae with 4 annulations, knee infuscate; inner, ventral aspect of profemora with 2 wide and 1 narrow maculations (Kauai I.) . . . . . roberti

The new species of Nesidiolestes (FIG. 1-5, 7-13)

Male and female: Length of male 6.9 mm; of female 8.1 mm (variation in paratypes: 6.9-7.7 mm, ♂♂; 8.0-8.2 mm, ♀♀).

Colorless in life, without any vestige of piceous or stramineous annulations on body or appendages, as are present on epigean species; subtranslucent, contents of

gut visible through abdominal wall; ♀ with a weak infuscation between eye and rostrum; ♂ sclerites of stapes visible through pygophore.

Body surface dull, excepting shining, weakly shagreened, glaborous areas on dorsum of thorax. Short, inconspicuous golden pubescence on head, thorax, abdomen, and appendages, sparser on abdomen.

Anteocular portion of head rather strongly convex above in lateral view (FIG. 5). First antennal segment over 4.7 x longer than head, its length 5.3 mm (♂) (variation in paratypes 5.2-5.5 mm), 5.4 mm (♀) (variation in paratypes 5.2-5.4 mm); relative length of antennal segments 11:10:3:4. Eyes strongly reduced to about 15 weakly pigmented facets; apparently not functional.

Meso- and meta-notum together longer than pronotum (6:4); mesonotum wider than long (4:3), metanotum wider than long (3.75:2.75), a short process at hind border of mesonotum only, mesonotal processes and metanotal spine, both knob-like, weakly developed.

Fore leg longer than body (16.8:14.5); fore coxa shorter than head and pronotum together (3.8:4.1); fore femur less than 2 x length of fore coxa (7.1:3.8), ventral spines much reduced in size (FIG. 5, 7), those on distal ½ barely discernable (on uncleared specimen), antero- and postero-ventral series of spines coalescent, not strongly differing in size, all spines decreasing in size apically, only the basal pair situated on wart-like processes, these much shorter than diameter of segment and with apices directed anteriorly. Tibia 3/4 as long as femur, its under surface with 2 conspicuous rows of inclined setae and a dense tuft of setae at apex. Fore tarsus 2-segmented, about 1/5 as long as fore tibia, basal segment 1/3 length of apical segment; meso- and meta-tarsus 3-segmented, claw lacking incised ventral lamella (FIG. 9).

Abdominal segments inconspicuously lobed. Shape of abdomen of ♂ as shown in FIG. 2, that of ♀ similar, though somewhat more widened toward middle; tergites

without small tubercles before center of hind borders; spiracular openings on raised tubercles. Genitalia of ♂ as shown in FIG. 10-13.

Late instar nymph: probably 5th instar (FIG. 3): (in glycerine) Differing from ♂ as follows: length about 5.0 mm; much paler, white in life, no infuscations. Pubescence generally shorter and sparser, a few scattered macrotrichiae on dorsum of abdomen. First antennal segment just exceeding 4 x length of head, its length 3.5 mm; relative length of antennal segments 7:6:1.8:4.2. Eyes strongly reduced, about 10-faceted.

Dorsum of thorax lacking knob-like processes; meso- and meta-notum together much longer than pronotum (2.9:1.1); mesonotum longer than wide (4:3), metanotum slightly longer than wide (9:8).

Foreleg longer than body (13:10); fore coxa shorter than head and pronotum together (27:31); fore femur less than 2 x length of fore coxa (49:27), ventral spines more strongly developed, but still very reduced on comparison with adults of congeners, basal pair with apices directed interiorly. Tibia 4/5 as long as femur. Fore tarsus about ¼ as long as fore tibia, ratio of basal tarsal segment to apical tarsal segment 10:13.

Abdomen very weakly sclerotized, not lobed, shape as shown in FIG. 3, lacking dorsal and spiracular tubercles.

Previous instar (in glycerine): also white in life. Based on exuviae of nymph described above and differing as follows; fore femur 2 x length of fore coxa, ventral spines still more strongly developed, the 1st 10 spines apical to the large basal pair situated on wart-like processes, apically sclerotized, ranging in total height from ½ to equal the height of the wart-like process of basal pair. Fore tarsus less than ¼ as long as tibia; ratio of basal tarsal segment to apical tarsal segment 5:16.

Distribution

Known only from Emesine and Alahaka Lava Tubes, Hawaii I.

Holotype ♂ (Bishop 10,261), allotype ♀, in copula (in alcohol), HAWAIIAN ISLANDS: Hawaii I., near Saddle Road, Emesine Lava Tube, 1700 m, 11.VII.1973, dark zone, F. G. Howarth and W. C. Gagné. Paratypes, 2 ♂♂, 4 ♀♀, 1 nymph and 1 exuviae, same data as holotype; 1 paratype, leg fragments, same data as holotype except, 10.III.1973, F. G. Howarth; 2 ♂♂, same data as holotype except, 14.II.1974, F. G. Howarth, N. C. Howarth and F. D. Stone.

Other material: 1 ♂, Hawaii I., Kau District, Kahuku Ranch, Alahaka Lava Tube, 2050 m, 10.VII.1973, dark zone, F. G. Howarth and W. C. Gagné (collected dead).

Etymology

A Hawaiian word for a cave or grotto is ana, geological structures used extensively by the ancient Hawaiians for shelter, food storage, and for burial of persons of high social rank. It is used as a noun in apposition. (The generic name means "little island robber.")

Discussion

Until the epigean species, especially N. selium, become better known the ancestor of N. sp. can only be conjectured. However, N. selium Kirkaldy is presumed to be the ancestral type of N. sp. This assumption is based on the similar reduced spination of the profemora of both species (FIG. 6, 7) and the fact that both are endemic to the island of Hawaii. The type localities of the 2 species are separated by about 25 km and 445 m altitude. There are no geographic barriers to separate the 2 species, so N. selium may occur in the rain forests adjacent to the lava flows containing populations of N. sp. Although N. selium is still known only from the type collected in 1896 there are indications in notes written by collector R. C. L. Perkins associated with other Nesidiolestes specimens from Oahu in the Bishop

Museum, that Kirkaldy misplaced some material. This may have included more specimens from the island of Hawaii. Epigean species of Nesidiolestes are extremely cryptic and may be nocturnally active, which could account for their paucity in collections.

It is interesting to note the allometry in the development of the profemoral spines in the 2 sequential nymphal instars available as compared with the adult. Although neoteny is a common trait of cavernicoles, this allometry would appear to be a case wherein ancestral (pleisomorphic) characters of the epigean progenitor are more pronounced in the endogean immatures and are progressively less pronounced in later instars. It will be most interesting to note whether these observations will be borne out with the availability of more material. Most authors have ignored nymphs in the preparation of emesine species descriptions. However, Readio (1927: 37, quoting Butler, 1923) noted that the hairs on the legs were longer than the adults in Empicoris vagabundus(L.), and McAtee and Mallock (1925:55) noted that in nymphs of Ploiaria setulifera McAtee and Mallock, "the armature of the fore legs was relatively stronger (especially in the bristling of the trochanter), more noticeably so in younger specimens."

Biology of Nesidiolestes sp.

Habitat.--Nesidiolestes sp. is known only from dark zones of 2 high altitude caves on Mauna Loa Volcano, island of Hawaii. Most collections and observations have been made in Emesine Lava Tube at 1760 m elevation. Fragments of a dead specimen of N. sp. also were collected from Alahaka Lava Tube, Kau, 2050 m elevation.

Emesine Lava Tube is a comparatively large cave with approximately 2 km of known passage. It is a relatively shallow lava tube, the overburden of rock being 1-2 m at skylights and possibly up to 4 m in lower passages. The cave is within the 1881 lava flow and is thus less than 100 years old. Both the air and water temperatures in the dark zone of Emesine Lava Tube vary between 14° and 15°C.

Water temperature was measured in small pools in the glazed lava on the floor.

At this elevation, the exposure and environment of an upper montane cloud forest would be expected. The annual precipitation surpasses 2500 mm, of which a large percentage occurs as fog drip. However, the surface above the cave is barren, dark young pahoehoe lava with scattered low shrubs and lichen. The lichen, which grows in cracks or in scattered patches, is the native Stereocaulon vulcani. The shrubs, up to 2 m tall, grow scattered 1-3 m apart, usually in cracks in the pahoehoe surface. The shrubs are the endemic Metrosideros collina, Coprosma ernodeoides, Vaccinium reticulatum, and Styphelia tameiameiae. A fern, Nephrolepis sp., also grows in cracks in company with the shrubs. The entrance sinkholes are very much richer in flora, especially mosses, lichens, liverworts, and ferns. Water percolates rapidly into the young substrate and evaporation from the dark surface is high, which leads to a xeric surface environment.

In contrast to the surface, the cave passage is constantly wet, and has occasional patches of thick roots extending 3 m from ceiling to floor. The roots most commonly are M. collina, although a few unidentified roots are also found. Apparently, the small shrubs are growing epiphytically on the new substrate and require large, deep root systems to maintain water balance on the xeric surface. The main energy source in the cave ecosystem is these roots.

Distribution in the cave.--In Emesine Lava Tube the bug has been found in many places throughout the cave, always in total darkness in rooms or small passages protected from air motion, with a saturated atmosphere and many tree roots. Most specimens were seen on the ceiling or hanging upside down on protuberances. One male was collected poised between 2 roots (FIG. 4). One adult was found in a small upper level side passage 450 m from the entrance. It was upside down in a small pocket 15 x 5 x 5 cm in the ceiling wall. Numerous small roots hung from the ceiling in the vicinity. The bug was observed for 1½ hours.

Food.--Feeding has not been observed and the natural prey is not known. Most likely N. sp. is a stationary predator. It selects a suitable location and waits for prey to approach within striking distance. However, it is possible that it may sometimes stalk its prey.

Potential prey in the cave are all stages of the cave planthopper Oliarus polyphemus Fennah and the cave moth Shrankia sp., the collembolan Protanura hawaiiensis Bellinger & Christiansen and other cave Collembola, small Diptera which appear to be accidental in the cave, and possibly small nymphs of the cave Orthoptera, Caconemobius sp. and Thaumatogryllus sp.

Observations in captivity are very limited. A dark spot in the abdomen presumed to be a food spot in the gut has been observed to move posteriorly in 2 individuals. On one occasion a N. sp. nymph possibly fed on a proffered aphid, as ascertained by the moving dark spot in the gut. Captive bugs did not feed on freshly killed small flies, Drosophila sp., and so do not appear to be scavengers.

Associated biota and food web.--The primary energy source in the Hawaiian cave ecosystem is tree roots. A preliminary food web for Kazumura Lava Tube, island of Hawaii, was presented by Howarth (1973). In general it also applies to these higher elevation caves, with a few notable exceptions, as follows: the large wolf spider, Lycosa howarthi Gertsch, has not been found in caves above 1200 m elevation and could possibly replace N. sp. as an efficient predator in the cave. Oliarus polyphemus Fennah (Homoptera) is not as common, this elevation apparently being close to the upper limit of its distribution. The cave millipede, Dimerogonus sp., and a centipede, Lithobius sp., are more common. The fruiting bodies of a basidiomycete, Pistillaria sp., are relatively common on the ceiling and walls and often not associated with roots. The "slimes" noted on the walls of Kazumura Lava Tube and caves lower in elevation on the island of Hawaii have not been found in Emesine Lava Tube, but this absence may be related to the youth of the cave.

Behavior.--Movement is slow, deliberate, one leg at a time. One individual required 15 minutes to climb 45 cm of tree root. Its antennae are characteristically held rigid, the 1st segment directed anterodorsad, the following segments bent anteroventrad. As the bug walks its antennae move back and forth only at the basal articulation. Thus the antennal apices swing up and down in front of the bug. During this rocking the apices of the antennae do not touch the substrate but stop approximately 1 mm before contact. When probed with a small root segment or with a finger the antenna also stopped 1 mm from the object. When either probe was moved to touch the antenna the bug retreated by rocking way back on its middle and hind legs. The antennae were held close to the body and the forelegs rotated back behind the head and extended slightly. The bug remained in this position and immobile for several seconds, then returned to walking randomly over the ceiling. This probing was repeated several times with the same results.

In the usual resting posture (FIG. 4) of N. sp., the fore femur and tibia are closely appressed and held at 90° to the longitudinal body axis at the side of the head anterior to the antennal bases. At other times, possibly in anticipation of prey, the fore legs are moved forward and held at 45° to the body axis in front of the head. In both stances the antennae are held still or rock slowly to and fro within the strike zone of the fore legs, as described above.

Specimens of N. sp. in the cave are not disturbed by a flashlight beam or by shadows and are apparently blind. They are strongly amenophobic and stenohygrobic, displaying negative taxis with weak air movement and becoming moribund with stronger air movement or with a decrease in humidity below saturation. The bug is initially disturbed by slow or minor changes in temperature but adjusts to the new temperature. A greater change, more than 5°C, elicits a similar moribund state to that displayed with a decrease in relative humidity. The initial negative response to temperature change is interpreted as the strong response to the decrease in relative humidity.

After a minor disturbance the bug commonly walks away while slowly rocking up and down. The body rocks down and slightly forward, then up and slightly back. Two such "pushups" are usually done per step. In one individual the "pushup" motion was performed after the first several disturbances (approximately 10 minutes). Then the bug walked slowly and randomly over the substrate without any rocking. The "pushup" motion returned when the bug was disturbed again after 5 minutes of no disturbance. This peculiar swaying motion when disturbed is characteristic of many Emesinae, although varying among species (Wygodzinsky 1966:55). The rocking of N. sp. is similar to a Bagauda sp. in caves in Thailand (Stone, pers. comm.).

Reproduction.--A mating pair of N. sp. was collected in a small upper level crawlway off the main passage in the dark zone in an area of numerous roots. The pair was on the ceiling hanging upside down and when disturbed moved slowly and randomly only a few decimeters. They were observed and photographed in situ for approximately 30 minutes, and then collected into a snap cap plastic vial, measuring 65 x 30 mm, which contained moist tissue paper. They were transported alive to the laboratory and observed several times during the day. They remained in copulation until they were removed from the vial for closeup photography the following day, 25 hours after collection. The disturbance during photography caused them to separate.

Wygodzinsky (1966:56) mentions that in the few Emesinae for which copulation has been observed the act may last several hours and may be repeated. It is possible that the pair separated during some of the 25 hours of captivity. However, this seems doubtful due to the slow movements of these cavernicoles and the fact that they were in copula and undisturbed during each of several observations during that time.

The position, as shown in FIG. 1, is the usual orientation, with the ♂ dorsal to the ♀. The body of the ♂ is held straight, the abdomen not noticeably bent at

base, and dorsal but not parallel to the ♀ body. The head is held at a distance dorsal to the ♀ metathorax equal to the length of the ♂ fore coxae. The raptorial fore legs of the ♂ grasp the legs of the ♀ near the base of the meso- and metatibiae. The ♂ antennae are closely appressed. Both first antennal segments are directed posteriorly over the body while the remaining segments are directed anteriorly, dorsal and parallel to the body. The ♂ abdomen is directed slightly to the right side of the ♀ abdomen. The pygophore is rotated 180° postero-anteriad so that the intromittant organ is directed anteriad into the ♀ genital opening.

The abdomen of the ♀ is arched slightly dorsad apically and oriented ventral and slightly sinistral of the ♂ abdomen. The raptorial legs and antennae of the ♀ are held in the usual resting posture.

The position is similar to that figured for Empicoris rubromaculatus (Blackburn) by Wygodzinsky (1966: plate 4, FIG. 3) except for the following in the latter species: the ♂ does not grasp the ♀ but rests its fore legs on the ♀ thorax, and the dorsoventral angle between them appears greater than in N. sp.

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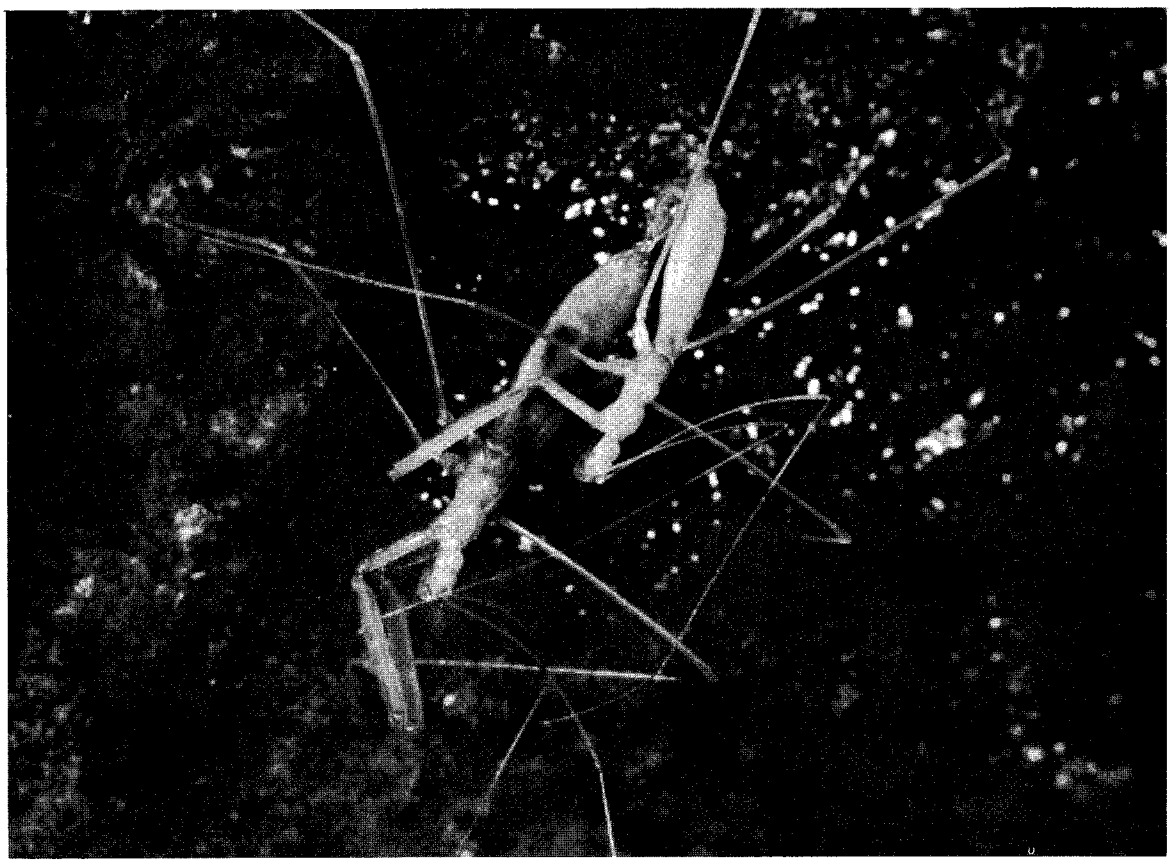


FIG. 1. Nesidiolestes sp. male below, female above in copula. Pair at onset of uncoupling presumably disturbed by photography. From photograph by W. P. Mull.

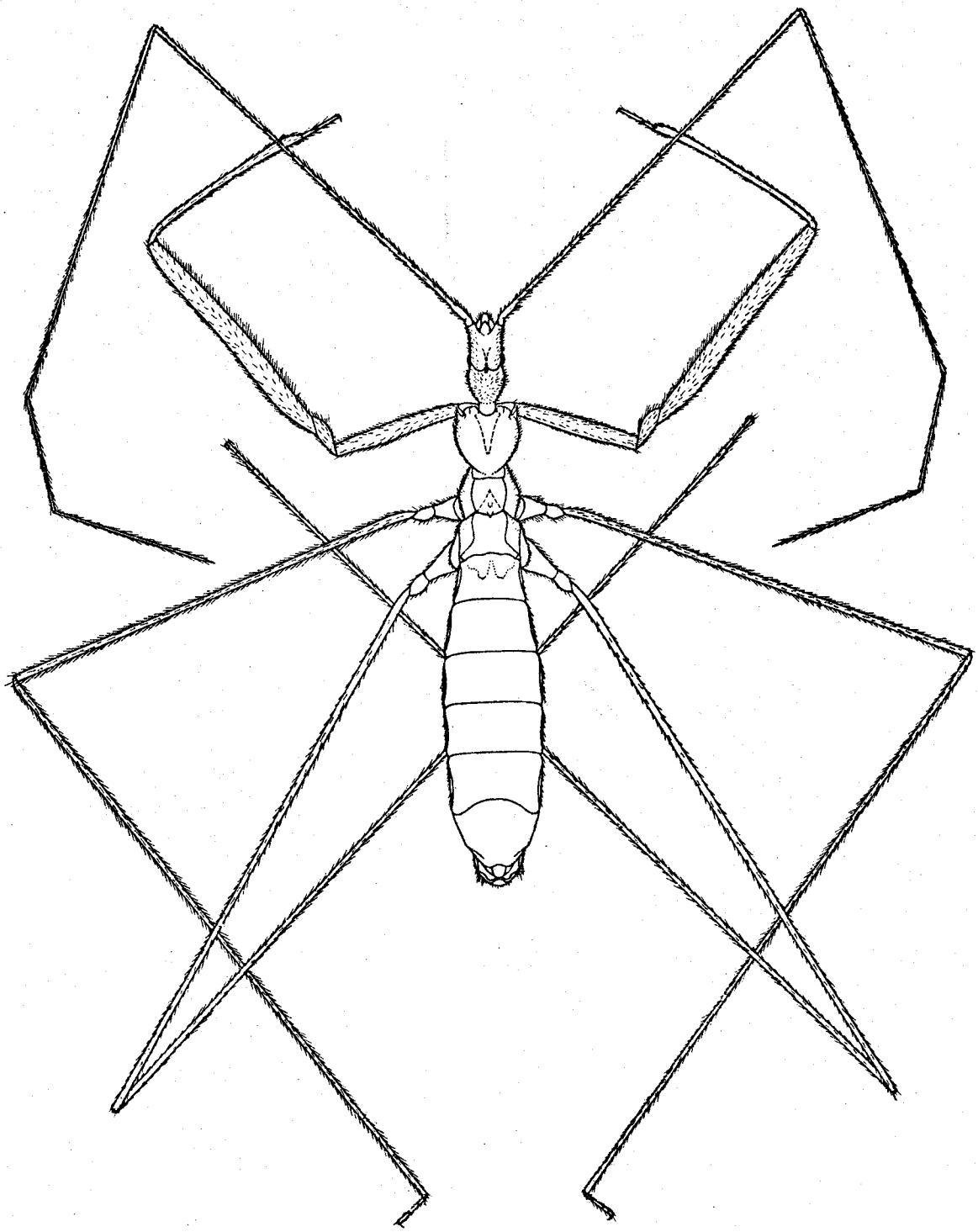


FIG. 2. Nesidiolestes sp., ♂: dorsal view (in fluid) (macrotrichae on dorsum omitted).

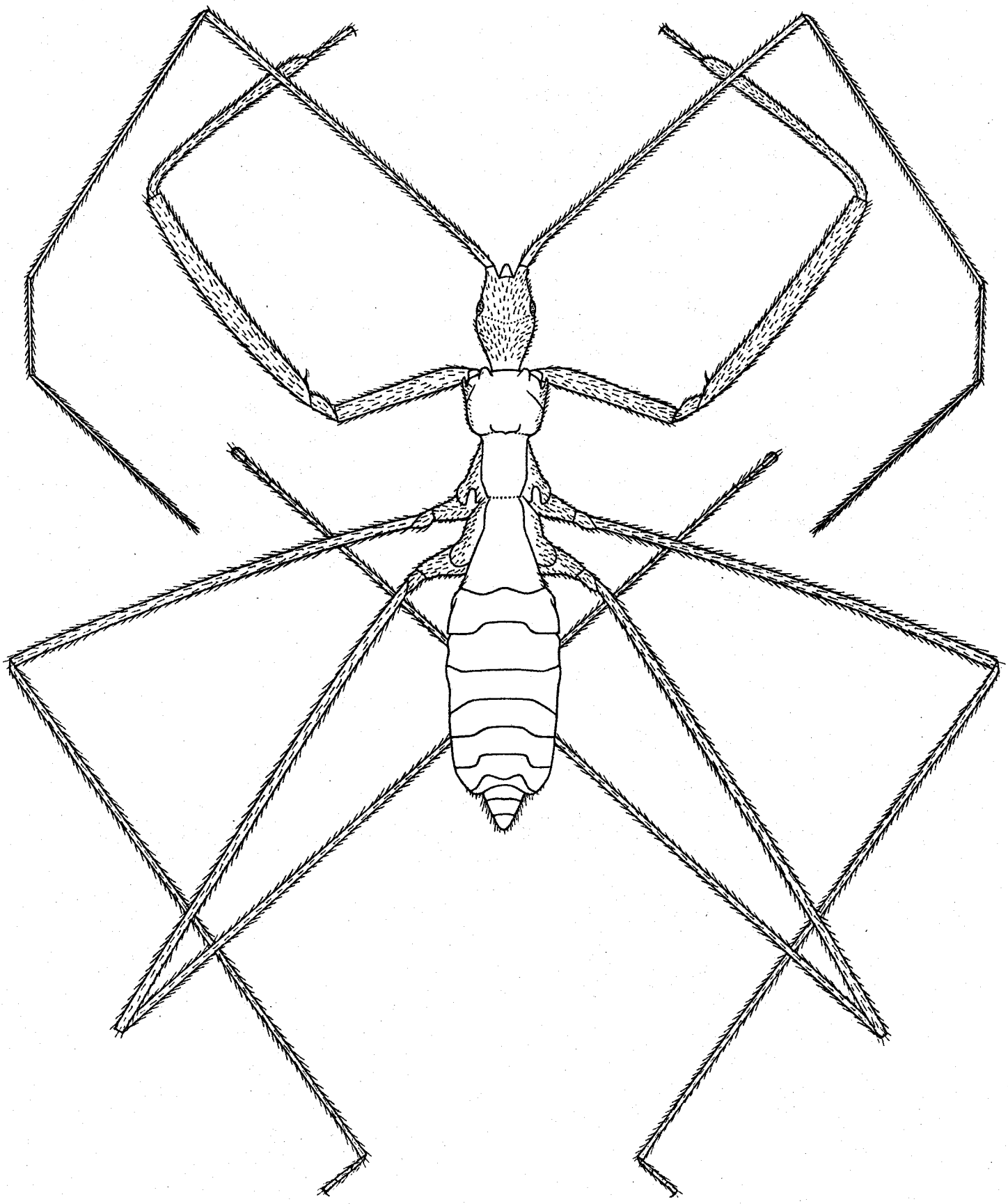


FIG. 3. Nesidiolestes sp., last instar nymph: dorsal view (in fluid) (macrotrichae on dorsum omitted).

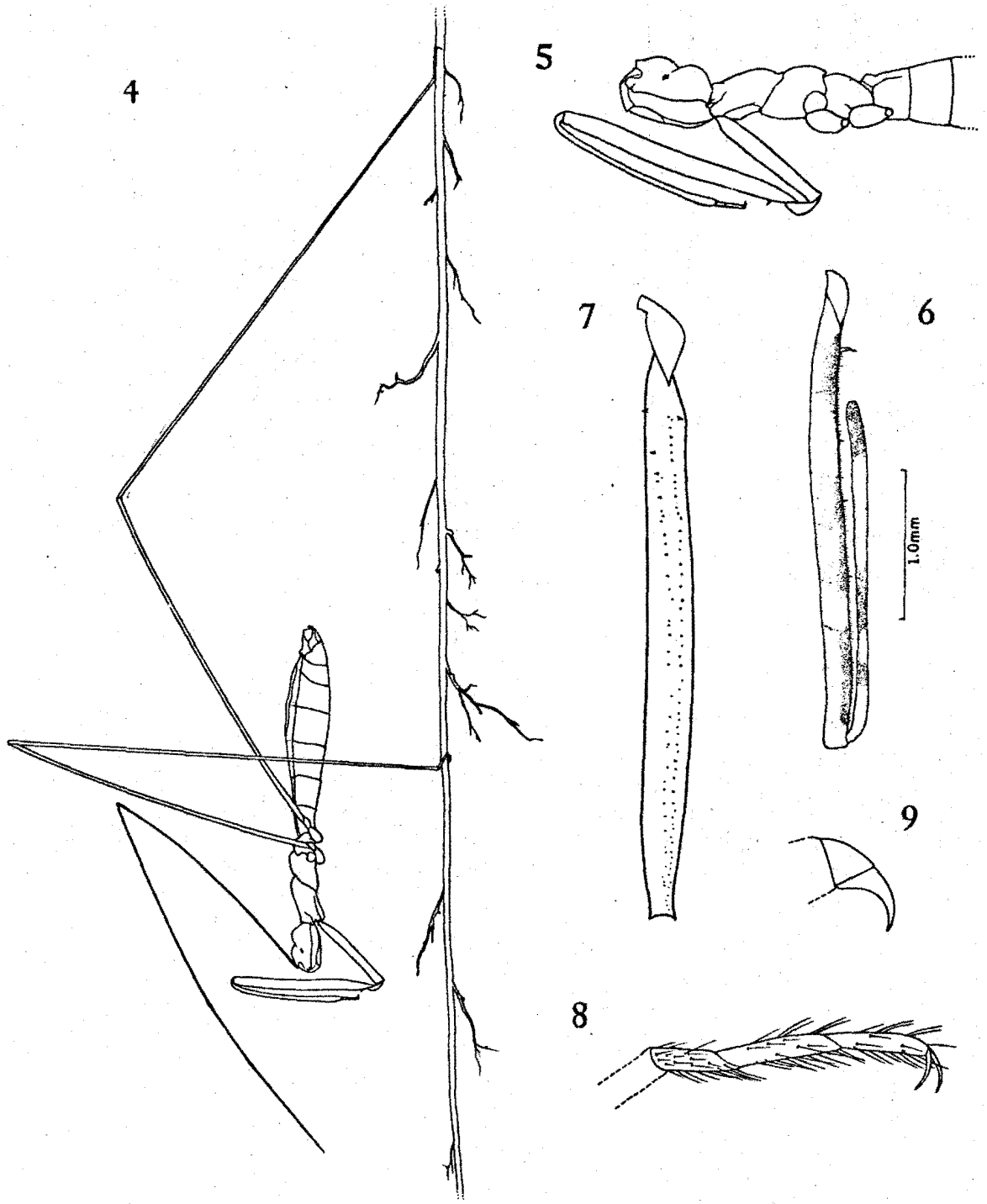
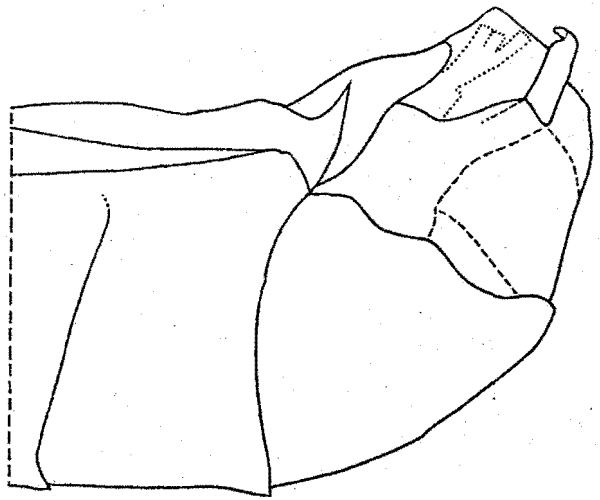
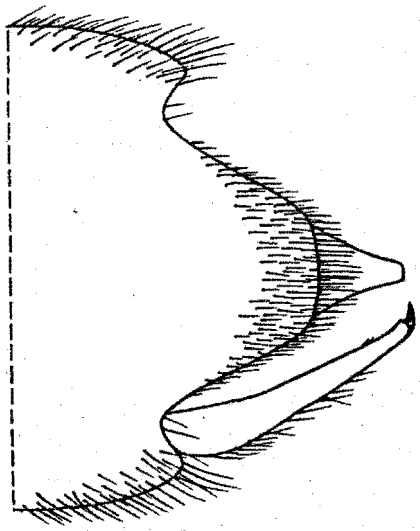


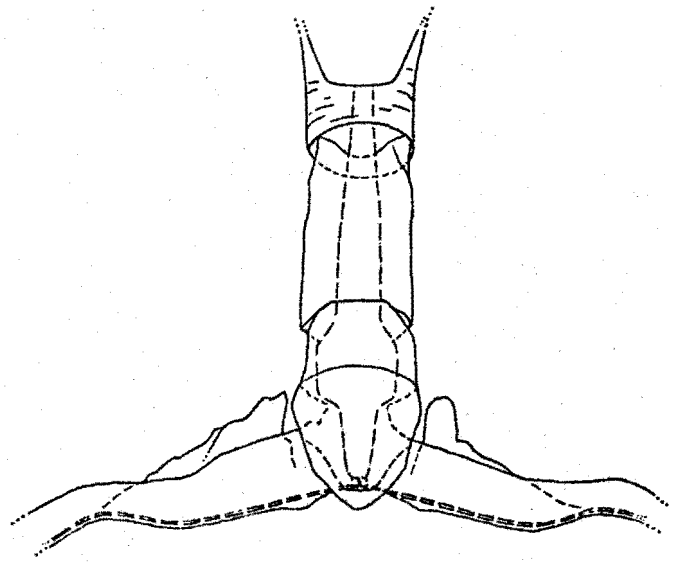
FIG. 4-9. Nesidiolestes sp., ♂: 4, hunting posture (drawn from photograph in habitat); 5, head, proleg and thorax, lateral view, setae omitted; 6, N. selium Kirkaldy, ♂: profemur and protibia, inner lateral view (drawn from sketch of holotype by G. Allan Samuelson); 7-9, N. sp., ♂: 7, profemur, ventral view; 8, hind tarsus, lateral view; claw of proleg, lateral view.



10



11



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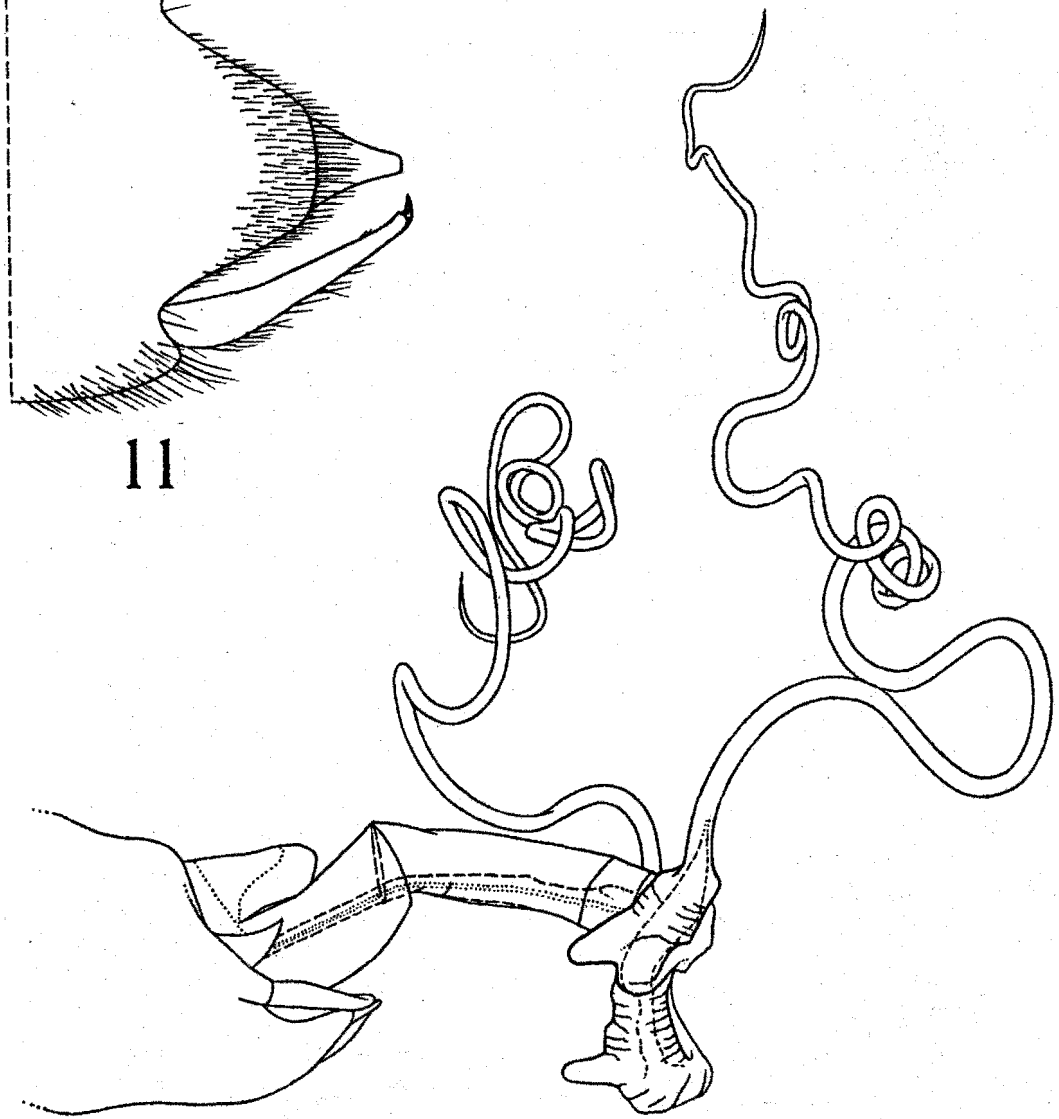

12

FIG. 10-13. Nesidiolestes sp., ♂: 10, genital segments, lateral view; 11, 9th abdominal segment and paramere, ventral view; 12, phallus and everted endosoma, ventrolateral view; 13, phallus and basal portion of arms of endosoma, dorsal view.

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